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Bite traces in a turtle carapace fragment from the middle Danian (Lower Paleocene) bryozoan limestone, Faxe, Denmark

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A fragment of a turtle carapace from the Middle Danian bryozoan limestone at the Faxe quarry, eastern Denmark, is identified as a partial costal plate from the carapace of a chelonoid turtle. The fragment bears traces of three separate acts of predation or scavenging. Two circular bite traces *Nihilichnus nihilicus* Mikuláš *et al.* 2006, 4 mm in diameter, situated 2.5 cm apart, are interpreted as crocodylian. Groups of parallel scrapes, *Machichnus bohemicus* Mikuláš *et al.* 2006, 4–5 mm long and 0.5 mm wide, are interpreted as bite traces from sharks. Small circular traces, ~1 mm in diameter, found either alone or in a row of three, are either from sharks or fish. This is the first record of turtles from the Danian bryozoan limestone exposed in Faxe quarry, and thus represents an important addition to the Danian vertebrate fauna of Denmark.

Key words: Turtle, Paleocene, Faxe bryozoan limestone, Stevns Klint Formation, predation, scavenging.

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Vertebrate skeletal remains are rare in the Danian bryozoan limestone of eastern Denmark. The described vertebrate fauna comprises 13 species of fish, based on otoliths (Schwarzhan 2003), and around 15 species of sharks (Jan Schultz Adolfssen, personal communication 2010). Marine crocodylians are known from single bones and isolated teeth (Bonde *et al.* 2008). Further indirect evidence of large vertebrates is found in the form of polished quartz pebbles interpreted as gastroliths (Noe-Nygaard 1975).

Sea-turtles are known from a collection of carapace fragments from the Upper Danian København Limestone Formation and Selandian Lellinge Greensand Formation (Dames 1897; Rosenkrantz 1920, 1921, 1923; Karl & Lindow in press). Three peripheral elements from the carapace of a marine turtle of the family Cheloniidae are known from the upper Maastrichtian limestone of the Tor Formation, Stevns Klint (Karl & Lindow 2009). Undescribed turtle remains are also known from the Danian limestone of the Limhamn

quarry, southern Sweden (Johan Lindgren, personal communication 2010).

Recently, a carapace fragment was found in the Faxe quarry, in a loose bryozoan bioclastic grainstone, together with abundant shark teeth and coprolites. This study describes this first occurrence of a marine turtle from in the middle Danian bryozoan limestone of Faxe and documents multiple sets of bite traces found on the carapace fragment.

Geological Setting

The large Faxe quarry located in south-eastern Sjælland, Denmark, (Fig. 1) contains well-exposed Lower Paleocene (middle Danian), bryozoan and coral limestone, which was deposited shortly after the mass extinction at the Cretaceous–Tertiary boundary during a relative rise in sea level (Thomsen 1976, 1983,

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1995; Surlyk 1997). The azooxanthellate scleractinian coral *Dendrophyllia* evolved and formed coral mound complexes in the epicontinental sea covering Denmark and southern Sweden (Floris 1980; Bernecker & Weidlich 1990, 2005; Willumsen 1995; Bjerager & Surlyk 2007a,b; Bjerager *et al.* 2010; Lauridsen & Damholt 2011).

The bryozoan mounds of the Danish Basin are skeletal deep-water mounds dominated by delicate bryozoan fragments and carbonate mud. They were formed in an outer-ramp setting, probably at the shelf-slope break of a distally steepened ramp (Surlyk 1997). The mound complex and the bryozoan mounds are situated over the easternmost part of the Ringkøbing-Fyn High and had a palaeolatitude of 45° N (Surlyk 1997).

The mounds are autochthonous and biogenically constructed (Cheetham 1971; Thomsen 1976, 1983; Surlyk 1997). The well preserved mound complex in Faxe comprises three main species of frame-building corals. The diversity of the associated fauna is very high with more than 250 species identified, including 30 non-constructional coral species (Gravesen 2001; Lauridsen & Damholt 2011). The invertebrates provided feeding grounds for a large population of vertebrates.

Material

The specimen was found by amateur geologist Alice Rasmussen in 1994 in the north-eastern corner of the Faxe quarry (Fig. 1). The specimen was collected but not given further attention until 2010, when one of the authors (JM) identified it as a fragment of a turtle carapace. The specimen is now catalogued as Danekræ (DK-627) and is part of the collection of the Natural History Museum of Denmark (MGUH 29293). It is currently on display in Geomuseum Faxe.

Order Testudines Linnaeus, 1758
Superfamily Chelonioidea Baur, 1893
Chelonioidea indet.

Description: The turtle material consists of a single irregularly rhomboid-shaped medial fragment of a costal plate, measuring 39 mm by 26 mm, with an average thickness of 4 mm (Fig. 2A–C). The dorsal surface is smooth and displays two shallow grooves delimiting the borders of the overlying unpreserved dermal scutes (Fig. 2A). The ventral surface is dominated by the sloping medial end of the rib head which is triangular in ventral aspect (Fig. 2B). The ventral surface of the rib slopes laterally, rapidly becoming confluent

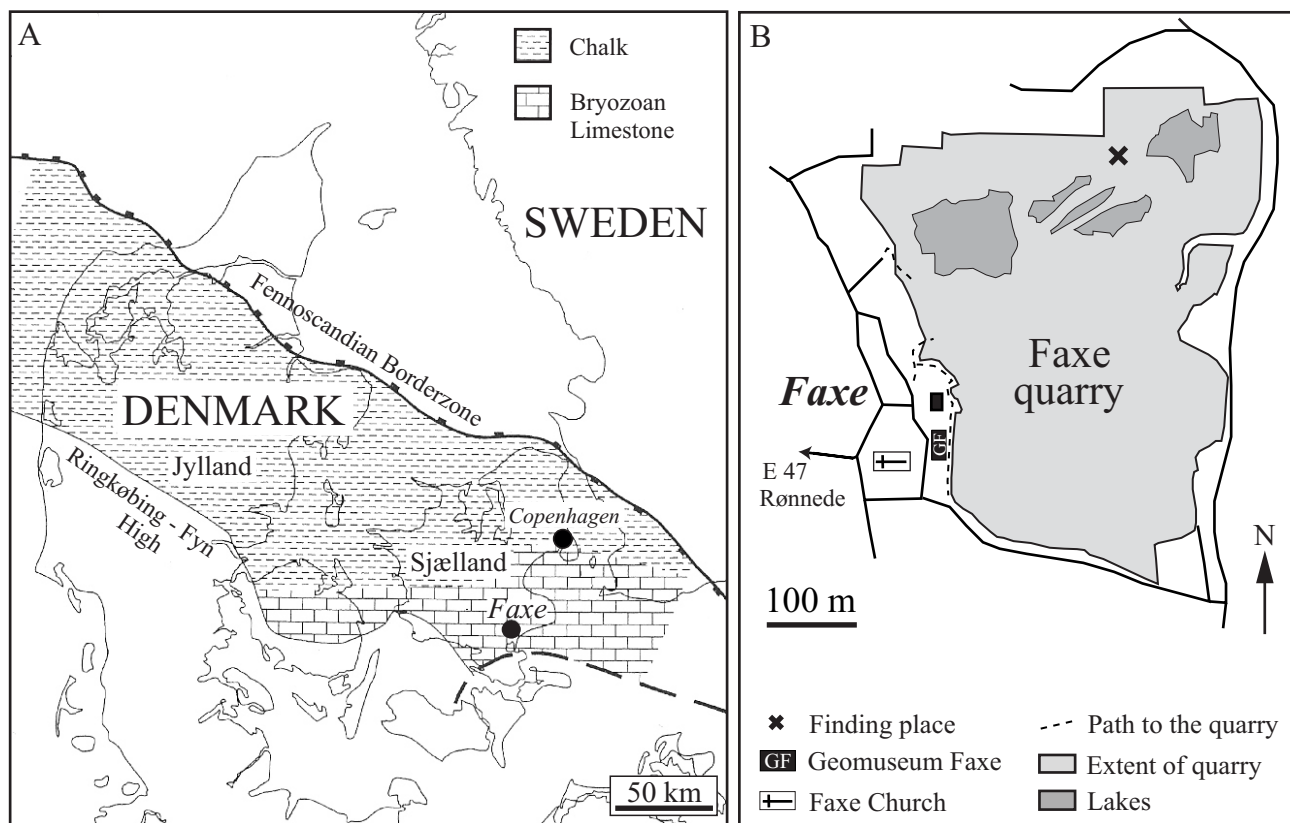


Fig. 1. **A**, Faxe quarry is located in the south-eastern part of the Danish island Sjælland, approximately 70 km south of Copenhagen. Modified from Schnetler *et al.* (2001). **B**, map of Faxe and Faxe quarry, with the finding place indicated.

with the ventral surface of the costal plate. The medial face of the rib end is lightly concave, opposite to the intervertebral region; the plate thins dorsally in this area (Fig. 2B). In addition, the presence of a wide scar for attachment of the medial end of the first rib (1Ra on Fig. 2B) identifies the specimen as the anteriormost costal plate from the left side of the animal (Fig. 3). Within turtles, from *Proganochelys* onwards, the first thoracic rib is the only one which is free and not incorporated into the carapace (Gaffney 1990); rather, it is attached immediately anterior to the medial head of the second thoracic rib (2Ra on Fig. 2B). Overall, the specimen is too fragmentary for a determination more specific than superfamily Cheloniioidea, family Cheloniidae or Toxochelyidae. The Dermochelyidae can be ruled out as the ribs in that family are fully separated from the shell plates.

Bite traces

Close examination of the specimen reveals several sets of bite marks which fall into three categories. On the dorsal side, two prominent rounded indentations in the shell are present (Fig. 2D, E); one hole is circular, measures 4 mm in diameter and has penetrated half-way through the bone (Fig. 2D). A second hole also 4 mm in diameter is present at the edge of the bone and has caused the bone to fracture (Fig. 2E). The distance between the two holes is 25 mm. A second type, also on the dorsal side, comprises groups of parallel, elongated scratch marks which have penetrated the surface of the bone; these marks are 3–4 mm long, 0.8 mm wide, and up to 0.5 mm deep (Fig. 2F, G). The third type comprises small rounded pits less than 1 mm in diameter and about 0.5 mm deep, found on the ventral side of the fragment. When seen in high magnification, the fragmented surface of the depressed bone can be seen in the bottom of the pits. The pits occur as individuals in rows of three (Fig. 2H, I).

Discussion

Bite traces or tooth marks in skeletal remains are well known from the zoological literature (e.g., Binford 1981; Brain 1981; Haynes 1980, 1983), and in recent years they have been studied increasingly in fossil material (Deméré & Cerutti 1982; Cigala-Fulgosi 1990; Schwimmer *et al.* 1997; Tanke & Currie 1998; Corral *et al.* 2004; Mikuláš *et al.* 2006; Jacobsen & Bromley 2009; Schwimmer 2010). Bite traces can originate from various behaviors ranging from predation (the deathblow,

slaughter and feeding) to subsequent scavenging including the later use of the skeletal parts as a source of calcium. Bite marks in the form of rounded pits, arising from perpendicular impression of teeth not penetrating the bone, have been given the ichnotaxonomic name *Nihilichnus nihilicus* Mikuláš *et al.* 2006. Parallel to sub-parallel scratches less than 1 mm wide are named *Machichnus bohemicus* Mikuláš *et al.* 2006, and are interpreted as gnawing traces formed while feeding on the soft tissue on the bone (Mikuláš *et al.* 2006).

The large predators known from the Faxe quarry and adjacent Danian limestone deposits comprise several genera of sharks and the marine crocodylian *Thoracosaurus*. Crocodylian teeth are not serrated and are circular in cross-section, whereas shark teeth are compressed, often serrated, and elliptical in cross section with sharp tips. *Thoracosaurus*, however, is a longirostrine crocodylian with long slender teeth, and it is uncertain if it could feed on turtles, but finds of isolated broader more cone-like crocodylian teeth suggest the presence of other brevirostrine crocodylians in the fauna. A recent study of bite traces from Dwarf Caimans preying on turtles shows that crocodylian bite traces include round puncture holes, *Nihilichnus*, as well as elongated, irregular scratches and large crushed areas from repeated bites to the same areas (Milàn *et al.* 2010). Fossil records of crocodylian-produced *Nihilichnus* in chelonian carapaces include a complete turtle skeleton from the Kimmeridgian of Eichstätt, Germany with abundant *Nihilichnus* and crushing of the carapace (Karl & Tichy 2004). *Nihilichnus* in chelonians has also been described from the Upper Cretaceous Blufftown Formation of Georgia and Alabama, USA (Schwimmer 2010). Here the bites are interpreted as originating from the giant Late Cretaceous crocodylian *Deinosuchus*, and similar traces are found in chelonian carapaces from the Paleocene of the Wannagan Creek quarry in Minnesota (Erickson 1984).

An alternative explanation has been suggested for the origin of *Nihilichnus*, especially in Mesozoic ammonites and nautiloids, as the result of limpet home scars dissolved into the aragonitic shells (Kase *et al.* 1998; Seilacher 1998). However, this interpretation is disputed by Kaufmann (2004) who retains the original interpretation by Kaufmann and Kiesling (1960) as predation by large vertebrates. In the case of bite traces in turtle shells, no alternative hypotheses have been suggested, as many modern crocodylians have a chelonivorous diet.

The large rounded bites traces in the Faxe specimen (Fig. 2D, E) are similar to the crocodylian bite traces interpreted from other fossil examples (Erickson 1984; Karl & Tichy 2004; Schwimmer 2010) and can, together

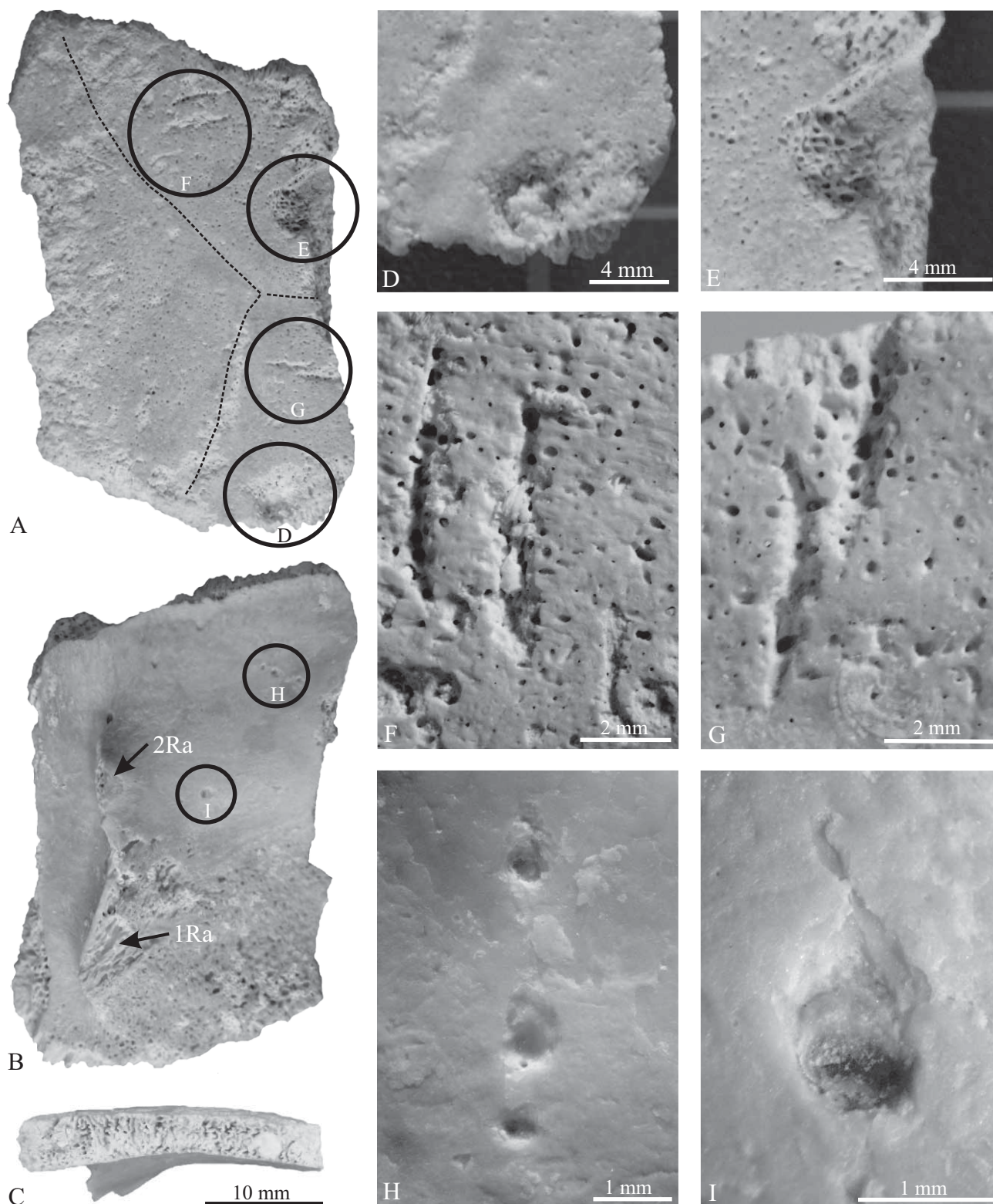


Fig. 2. **A**, dorsal view of the carapace fragment (MGUH 29293). The shallow grooves (indicated by thin broken lines) show that the fragment is a costal plate. **B**, ventral view of the plate with visible attachment scars for the ribs; 1Ra: attachment of 1st thoracic rib; 2Ra: attachment of 2nd thoracic rib. **C**, the costal plate in posterior view, showing the slight curvature of the carapace. A–C are reproduced to the same scale; circled areas refer to D–I. **D**, large bite, *Nihilichnus nihilicus*, that has penetrated halfway through the bone. **E**, large bite which has caused the carapace to fracture. **F**, three small parallel scratches, *Machichnus bohemicus*, which have penetrated the surface of the bone. **G**, two small subparallel *Machichnus bohemicus*; the scratches are morphologically similar to those in F. **H**, row of three small bites, *Nihilichnus nihilicus*, in the ventral side of the carapace fragment. **I**, single small *Nihilichnus nihilicus* in the bone. Note the crushed bone in the bottom of the pit.

with the small round traces (Fig. 2H, I), confidently be assigned to *Nihilichnus nihilicus* Mikuláš *et al.* 2006. They are likely to be the result of predation by crocodylians, as crocodylian remains are documented from the Faxø quarry (Bonde *et al.* 2008) and the adjacent Limhamn quarry (Troedsson 1923, 1924). The parallel to sub-parallel scratches appear as sharp cuts in the bone surface (Fig. 2F, G) and are morphologically similar to bite traces from sharks recorded in the bones of Pliocene dolphins (Bianucci *et al.* 2010) and marine turtles from the Cretaceous (Schwimmer *et al.* 1997; Shimada & Hooks 2004), and are referred to *Machichnus bohemicus* Mikuláš *et al.* 2006.

On the basis of the ichnological evidence, a scenario for the fate of the turtle is as follows. The large bites, *Nihilichnus nihilicus*, are primary predation marks from a crocodylian crushing the carapace, which was fatal to the turtle. The smaller scratches, *Machichnus bohemicus*, and pits are the result of subsequent cleaning of the carcass by smaller scavengers, most likely small sharks and carnivorous fishes.

Conclusion

A costal plate fragment from a marine turtle carapace is the first record of turtles in the middle Danian bryo-

zoan limestone exposed in the Faxø quarry and in correlative layers elsewhere in Denmark, and thus forms an important addition to the sparse Danian vertebrate record of Denmark. The presence of the attachment scar of the free anteriormost thoracic rib identifies the plate as the anteriormost costal plate from the left side of the animal. Due to the fragmentary nature of the specimen it can only be confidently referred to the superfamily Cheloniioidea. The carapace fragment bears evidence of predation by a crocodylian and subsequent gnawing by small scavengers such as sharks and fish.

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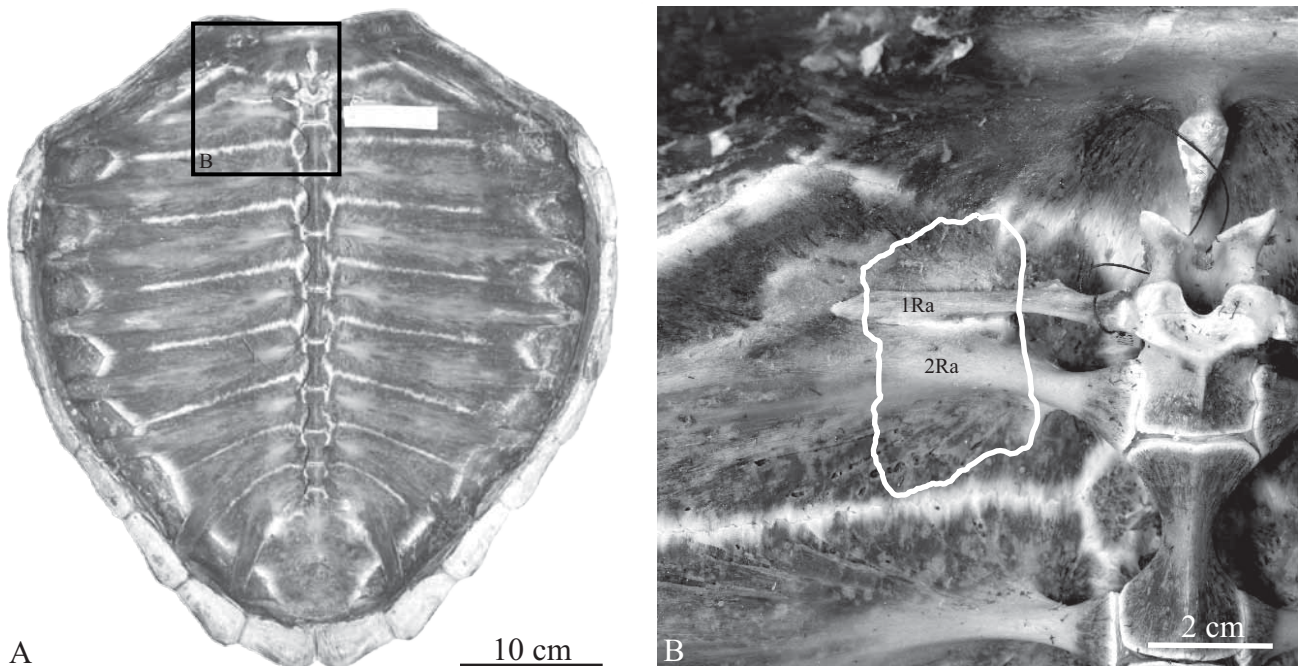


Fig. 3. **A**, ventral view of the carapace from a modern marine turtle *Caretta caretta* of the family Cheloniidae, from the Natural History Museum of Denmark (R2726). **B**, enlarged section showing the position of the fossil specimen, with the corresponding rib attachments indicated.

Dansk sammendrag

Det første kendte stykke af skjoldet fra en havskildpadde er blevet fundet i bryozokalken i Faxe Kalkbrud (Fig.1). Stykket blev fundet af Alice Rasmussen i 1995, men blev først identificeret i 2010. Stykket måler 39 x 16 mm, er 4 mm tykt og er svagt buet. På oversiden af stykket ses en svag fure, der markerer kontakten mellem tre af de overliggende hornplader, der ikke er blevet bevaret (Fig. 2A–C). På undersiden af stykket ses to ribbensfæster, der viser, at det er den forreste rygplade fra skjoldet, da det kun er den forreste rygplade i et skildpaddeskjold, der har to ribbensfæster (Fig. 3). Det er ikke muligt at identificere stykket nærmere end overfamilien Chelonioida, som omfatter de moderne havskildpadder. Stykket er det første kendte eksemplar af en havskildpadde i det mellemste Danien i Danmark. Derudover viser stykket en dramatisk historie, idet der er tre forskellige typer af bidemærker i det. Den første type består af to cirkulære huller, 4 mm i diameter med en afstand på 25 mm mellem sig (Fig. 2D, E). Disse bidemærker henføres til ichnoslægten *Nihilichnus nihilicus* Mikuláš *et al.* 2006. Et af disse bidemærker er placeret på en brudflade i stykket. Det er sandsynligt at pladen er blevet knust af dette bid (Fig. 2E). Disse huller tolkes som bidemærker fra en krokodille, da disse har tænder med cirkulært tværnsnit og hullerne er magen til både fossile og recente eksempler, hvor krokodiller har spist skildpadder. En anden type bidemærker består af parallelle til sub-parallelle furer 4–5 mm lange og 0.5 mm brede, *Machichnus bohemicus* Mikuláš *et al.* 2006, som stammer fra hajer der har raspet kød af skjoldfragmentet (Fig. 2F, G). En sidste type små *Nihilichnus nihilicus* omkring 1 mm i diameter optræder enkeltvis og i en gruppe af tre på en række. Man kan se knusning af knoglevævet i bunden af disse, og de formodes at stamme fra enten hajer eller fisk (Fig. 2H, I). Baseret på bidemærkerne kan følgende forløb for skildpaddens skæbne opstilles: Først er den blevet angrebet af en havkrokodille, der har knust skjoldet og dræbt skildpadden. Dernæst har små hajer og fisk raspet skjoldstykkerne rene for de sidste kødrester, inden det blev begravet i havbunden. Stykket er erklæret for Danekræ (DK-627), da det er det første stykke af en havskildpadde, der er fundet i det mellemste Danien i Danmark, og da det afslører en forhistorisk interaktion mellem rovdyr, byttedyr og ådselsædere.

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